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Impacts of temperature, hunger and reproductive condition on metabolic rates of flower-dwelling crab spiders (Araneae: Thomisidae)

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Abstract. Temperature strongly affects spider metabolic rate. Consequently, quantifying a species' temperature-metabolism relationship is useful in evaluating consequences of choices that affect body temperature. Body size also influences metabolic rate, and body size in spiders is strongly impacted by feeding and reproductive condition. Using adult female crab spiders, *Misumenoides formosipes* Walckenaer 1837 and *Mecaphesa asperata* (Hentz 1847) (formerly *Misumenops asperatus*) acclimated to field ambient conditions, I measured standard metabolic rates (SMR) over an ecologically relevant temperature range (10–40° C). I controlled hunger and reproductive condition of *M. formosipes* using starved (25 days post-feeding) or fed (7 days post-feeding) spiders, and virgin or mated spiders; in experiments with *M. asperata*, I used fed spiders of unknown reproductive status. Temperature strongly affected crab spider SMR, and both species showed similar temperature-SMR relationships. *Mecaphesa asperata* displayed equivalent temperature coefficients (Q_{10}s – the factor by which a physiologic process changes with temperature) for SMR across the experimental temperature range, while *M. formosipes* had significantly higher Q_{10} at low temperature than at mid-range or high temperature; Q_{10}s of the two species reflected previously determined impacts of temperature on hunting performance. Influence of hunger-reproductive condition on SMR of *M. formosipes* depended on how I accounted for body size; regardless of method, gravid spiders did not show elevated metabolic rate. Lastly, I combined crab spider SMR data with published SMR data to generate mass-metabolism equations for spiders; mass-scaling exponents approximated 0.67.

Keywords: Body size, mass scaling, Q_{10}, SMR, starvation

Respiratory metabolism describes an animal's cost of living. In spiders that ambush prey using a sit-and-wait strategy rather than a web trap, foraging costs approximate standard metabolic rates (Riechert & Harp 1987). Consequently, such spiders may serve as useful models for elucidating the impacts of various factors on metabolic rate and subsequent fitness.

Temperature and body size are the most important variables affecting metabolic rate (Meehan 2006; Gillooly et al. 2001). Temperature is a keystone variable that exerts pervasive effects at all levels of biological organization (Hochachka & Somero 1984), and its impact on an animal's physiological capacities ultimately affects performance and fitness (Huey & Kingsolver 1989). The influence of temperature on metabolic rate has been thoroughly confirmed in insects (Chown & Nicholson 2004) and spiders (Anderson 1970; Moulder & Reichle 1972; Moeur & Eriksen 1972; Seymour & Vinegar 1972; Humphreys 1975; Shillington 2005). Most spider studies have used animals acclimated to a particular temperature. I quantified temperature impacts on SMR of adult female crab spiders, *Misumenoides formosipes* and *Mecaphesa asperata*, acclimated to naturally fluctuating field conditions. Both spiders are diurnally active ambush predators that hunt on flowers, and temperatures of their floral microhabitats can exceed ambient temperature (T_a) by 10° C or more (Schmalhofer 1996). Consequently, *M. asperata* and *M. formosipes* may experience widely varying temperature over the course of a day. Previous work has shown that the two species respond differently to temperature: *M. formosipes* hunts well from 15–40° C, but experiences a sharp decline in hunting performance at 10° C, whereas *M. asperata* hunts equally well from 10–40° C (Schmalhofer 1996; Schmalhofer & Casey 1999); *M. formosipes* also tolerates and prefers higher temperature than *M. asperata* (Schmalhofer 1999). I predicted that SMR would increase with increasing temperature in both species and that Q_{10}s would reflect the pattern shown by spider hunting performance (i.e., consistent Q_{10}s over temperature intervals where hunting performance was consistent, higher Q_{10}s over temperature intervals where hunting performance declined).

Although the impact of body size on spider metabolic rate has been well established (Greenstone & Bennett 1980; Anderson & Prestwich 1982; Anderson 1996), the complicating factor of reproductive condition has not been addressed. In female spiders, reproductive state strongly influences mass. Hence, a spider's reproductive condition could potentially affect metabolic rate. Kotiaho (1998) proposed that metabolic rate differs with reproductive condition among female spiders, and Walker & Irwin (2006) suggested that reproductive females would have higher metabolic rates than non-reproductive females. These hypotheses have not been tested. In this study, I quantified SMR of adult female *M. formosipes* in various states of hunger (fed or starved) and reproductive condition (virgin or mated). I predicted that although whole animal SMR would increase with increasing spider mass, mass-specific SMR would be equivalent among *M. formosipes* of differing hunger-reproductive condition (null model).

Many studies have generated mass-metabolism equations for particular spider species or families, for spiders in general, and for broader taxonomic categories, such as arthropods and ectotherms. I combined the mass-metabolism data obtained for *M. asperata* and *M. formosipes* with published data to generate a compilation data set, which I used to evaluate the mass-metabolism relationship of spiders in general. Although most studies have used adult female spiders to determine size-metabolism relationships, reproductive condition has not been explicitly considered. I compared SMR estimates, generated

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Table 1.—Field ambient temperature (T_a) preceding the measurement of crab spider SMR. I obtained temperature data (° C) from the Hutcheson Memorial Forest Research Center, Somerset County, New Jersey. I calculated average daily T_a from daily high and low T_a measurements. Average difference was based on the difference between a given day's high and low T_a (range: 6–24° C for both species). Maximum difference was the difference between the highest high T_a and lowest low T_a during a particular time period. Values in parentheses are ± 1SD.

Time frame	Average daily T_a	Average difference	Temperature range		Maximum difference
			Daily high	Daily low	
Spring 1994					
Collection to testing May 16–July 4 (50 days)	19.9 (4.8)	14.4 (4.3)	13.3–35.0	1.1–20.6	33.9
Two weeks prior to testing June 21–July 4 (14 days)	23.3 (1.8)	11.6 (4.0)	26.7–32.2	11.7–19.4	20.5
Summer 1994					
Collection to testing July 25–Sept. 18 (56 days)	20.4 (3.7)	13.7 (3.8)	21.1–32.2	3.9–20.6	28.3
Two weeks prior to testing Sept. 4–18 (14 days)	18.1 (3.3)	16.1 (2.8)	22.8–31.1	3.9–17.2	27.2

by published mass-metabolism equations and equations derived in the current study, with measured SMR values for crab spiders to assess the utility of the various equations in predicting SMR. I tested the null hypotheses that equation-generated estimates would not differ from measured SMR and that the equations would not differ from one another in their predictive ability.

This study is the first to examine the impacts of temperature on spiders acclimated to naturally fluctuating field conditions and to evaluate the joint influences of hunger, reproductive condition, and temperature on SMR. Results of this investigation will permit future estimations of foraging costs in field populations.

METHODS

Study animals.—*Misumenoides formosipes* and *M. asperata* are sit-and-wait predators that use enlarged, raptorial forelimbs, rather than a web, to capture prey. These spiders are widely distributed throughout North America (Gertsch 1939), semelparous, and have a lifespan of one year. Adults are seasonally separated: in central New Jersey, *M. asperata* matures in April–May, while *M. formosipes* matures in mid-August. I used only adult female spiders in this study and collected spiders from three field sites in Middlesex County and two field sites in Somerset County, New Jersey, USA. I did not consider population of origin as a factor in my analyses, although it is likely that experimental spiders represented two or three distinct populations for each species. Voucher specimens reside at the American Museum of Natural History, New York.

I kept spiders in small vials, plugged with moistened cotton balls, in a shaded, well-ventilated, outdoor enclosure. Consequently, spiders experienced field T_a, which varied over the course of a day and from time of collection to time of testing (Table 1). I fed spiders 2–3 flies (muscids and calliphorids; fly mass ≈ 25 mg) per week, which is comparable to the rate of prey capture in the field (Schmalhofer 2001). The amount of food in a spider's gut approaches zero after six days fasting (Nakamura 1972, 1987); in order to preclude variations in metabolic rate resulting from the absorption of food from the gut (Anderson 1970), I withheld food from "fed" spiders for seven days prior to measuring SMR. "Starved" *M. formosipes* fasted 25 days prior to testing, a time span that should have allowed metabolic rates to stabilize after any decline induced by starvation (Anderson 1974).

Experimental temperature range.—I tested spiders over an ecologically relevant temperature range: 10–40° C (*M. asperata* at 5° C intervals, *M. formosipes* at 10° C intervals). During May and June (i.e., when penultimate instar and adult *M. asperata* are active), daytime high T_a averages (mean ± SD) 25.1 ± 5.2° C, while nighttime low T_a averages 10.7 ± 5.2° C. Daytime high T_a from mid-July through mid-September (i.e., when penultimate-instar and adult *M. formosipes* are active) averages 29.4 ± 3.5° C, while nighttime low T_a averages 15.0 ± 4.6° C. (I determined averages using daily high/low temperature measurements taken at the Hutcheson Memorial Forest Research Center, Somerset County, New Jersey, from 1993 to 1995.) Compared to *M. asperata*, *M. formosipes* experiences an approximately 5° C upward shift in diurnal and nocturnal T_a. Because both *M. asperata* and *M. formosipes* may experience higher-than-ambient daytime temperatures due to the sun-exposed nature of their floral hunting sites, a temperature range of 10–40° C describes much of the thermal variation typically experienced by adult spiders in the field (Schmalhofer 1996).

Hunger and reproductive condition.—*Mecaphesa asperata* matures in early spring, and timing of maturation in this species is not as well-synchronized as it is in *M. formosipes*. The *M. asperata* I collected did not molt during their time in captivity, indicating that they were adults when collected. Consequently, I only examined temperature impacts on SMR in this species. The early work with *M. asperata* suggested, however, that it would be interesting to examine the impact of body size on SMR more thoroughly, and manipulating hunger state and reproductive condition provided a mechanism to generate a wide range of spider body sizes.

Controlling for hunger and reproductive condition of *M. formosipes* resulted from a combination of random and non-random assignment of treatments. Using a 2×2 design, I established four hunger-reproductive conditions of *M. for-*

mosipes: fed-mated, fed-virgin, starved-mated, and starved-virgin. I assigned spiders collected from the field as adults to the fed-mated category; spiders collected as juveniles I assigned to the fed-virgin, starved-virgin, and starved-mated categories. *Misumenoides formosipes* collected as adults were either clearly egg-heavy (spiders collected in September, $n = 2$) or did not appear obviously pregnant (spiders collected in mid-to-late August, $n = 2$). Although female crab spiders mate soon after reaching maturity, typically within 1–2 days (LeGrand & Morse 2000; Morse 2007), I provided adults collected in mid-to-late August with the opportunity to mate, just to be certain. In my experiments, I intended that fed-gravid spiders represent the higher end of the size (mass) spectrum that *M. formosipes* was capable of achieving. Mated spiders eating a normal field diet (which included large prey, such as honeybees and bumblebees) achieved much larger body mass that did mated spiders fed the captivity diet of muscid and calliphorid flies (Schmalhofer, pers. obs.). In order to maximize mass as much as possible, I marked the adults collected in mid-to-late August, released them back into the field, and recollected them in early September once they had achieved an "egg-heavy" appearance. I manipulated the reproductive condition of sub-adult females (spiders collected in late July and early-to-mid August, $n = 11$) by randomly assigning them to be mated or not once they underwent their final molt. Mass and SMR of starved-mated and starved-virgin *M. formosipes* did not differ (Mann-Whitney *U*-tests, P = NS in both cases), therefore I combined these spiders, and subsequent analyses dealt with only three categories: starved, fed-virgin, and fed-gravid. I used the term "gravid" to denote the extremely egg-heavy condition of fed-mated individuals.

Duration of captivity did not appear to affect the maturation schedule of *M. formosipes*. The spiders used in the present study were part of a much larger group of spiders ($n = 173$) collected for use in other experiments, and approximately half of these spiders underwent their final molt between the 15th and 25th of August. Spiders collected at different times (July 25–29, July 30–August 5, August 6–12) showed similar proportions (54–63%) of individuals molting during the August 15–25 period.

Metabolic rate measurement.—I determined SMR during daylight hours over a two-day period for each species. Spiders were resting, fasting (i.e., post-absorptive), and the test-range of temperatures (10–40° C) fell within the tolerance limits of both species (Schmalhofer 1999). Consequently, metabolic rate measurements satisfied the criteria for SMR (IUPS 2001). Although some spider species show temporal variation in oxygen consumption (Anderson 1970), I did not expect *M. asperata* and *M. formosipes* to do so because they hunt both diurnally and nocturnally (Schmalhofer 1996). SMR obtained for *M. formosipes* and *M. asperata* in the present study were comparable to the nocturnally measured SMR obtained by Anderson (1996) for *M. formosipes* and *Mecaphesa celer* (Hentz 1847), respectively.

A respirometer chamber consisted of a 60-cm^3 syringe with an attached three-way valve. Prior to spider placement, I pumped a syringe twice to flush the air inside. After introducing a spider, I expelled as much air as possible from the syringe (without squashing the spider – interior volume reduced to 3 cm^3), then drew room air into the syringe to a volume of 60 cm^3 and closed the valve. I collected control samples (empty syringes containing only a 60 cm^3 sample of room air) in the same manner. I placed spider and control syringes in a temperature box, where they remained for 2–5 h. I recorded time and barometric pressure both when spiders were placed in and removed from the temperature box.

I used an Amitek S-3A oxygen analyzer equipped with an N37 medical sensor to measure oxygen content of air samples. Both cells of the sensor had tygon tubes attached (≈ 2 m length, 0.32 cm inside diameter), and air drawn through each line passed through a separate desiccant (drierite) tube; I injected air samples into line 2 via a three-way stopcock. An R-2 flow controller (Amitek) maintained flow rate at 40 ml min^{-1} in each channel. To test an air sample, I closed the stopcock connected to line 2 and measured baseline delta (channel one minus channel two); I then drew a 40 cm^3 sample of air from a spider or control syringe into a sampling syringe, connected the stopcock on the sampling syringe with the stopcock on line 2, opened both stopcocks and injected the air sample into channel two of the oxygen analyzer. Injection of an air sample took less than 1 second and flushed the entire tygon tube of room air, replacing it with sample air. The large pressure transient disappeared within a few seconds, followed by a return to baseline. Delta max occurred about 1 min later and remained stable for approximately 1 min, then gradually returned to baseline as the sample washed out of the tube and room air replaced it. After injection of an air sample, it took approximately 3 min for the S-3A readout to peak and return to baseline. I tested air samples at 4–5 min intervals and interspersed measurement of spider samples with control samples. I calculated SMR as oxygen consumption ($\dot{V}_{O_2}$) in μl h^{-1} corrected to standard temperature and pressure dry (STPD) conditions using the equation of Bartholomew & Casey (1978). For STPD corrections, I used average barometric pressure based on barometric pressure when spiders were placed in and removed from the temperature box. I weighed spiders immediately prior to placement in the syringes.

Open system (flow through) respirometry with real-time measurement of O_2 consumption or CO_2 production has become the preferred method for measuring metabolic rate. The advantage of open system respirometry is the ability to factor out active periods, permitting more accurate measurement of SMR. Closed systems, such as the one used in my study, require the measurement of metabolic rate over prolonged intervals and may incorporate both active and inactive periods, leading to overestimation of metabolic rate (Lighton & Fielden 1995). In the case of spiders, however, closed and open system respirometry yield similar results (Lighton & Fielden 1995). Crab spiders in particular are extremely sedentary, negating the need to factor out periods of elevated metabolic rate caused by bouts of activity: once placed in a small container, *M. asperata* and *M. formosipes* quickly settle down, assuming the classic, stationary, crab spider hunting posture, and remain motionless for hours at a time.

I measured $\dot{V}_{O_2}$ for each spider at each test temperature. Because regression lines for *M. asperata* using data collected at 5° C intervals and 10° C intervals were nearly identical, I tested *M. formosipes* at 10° C intervals. For each species, I measured

metabolic rate near the end of the time frame in which adult female spiders were typically found in the field: *M. asperata*, early July; *M. formosipes*, mid-September.

Temperature and crab spider SMR.—I used linear regression to generate equations describing the relationship between temperature and mass-specific $\dot{V}_{O_2}$: I calculated regression equations for each individual, each species, and for each hunger-reproductive condition of *M. formosipes*. Using ANCOVA, I compared the mass-specific $\dot{V}_{O_2}$-temperature relationships shown by these crab spiders to one another and to published data for other spider species.

Temperature coefficients.—I calculated Q_{10}s for each species and for each *M. formosipes* hunger-reproductive condition at low temperature (10–20° C), mid-range temperature (20–30° C), and high temperature (30–40° C). Using Kruskal-Wallis tests, I compared Q_{10}s within a species across the experimental temperature range, and, within a given 10° C interval, I compared Q_{10}s among *M. formosipes* hunger-reproductive conditions. Where Kruskal-Wallis tests were significant, I made *a posteriori* pair-wise comparisons using Mann-Whitney *U*-tests.

Impacts of temperature, hunger, and reproductive condition on SMR of *M. formosipes*.—To assess joint impacts of temperature, hunger and reproductive condition on mass-specific $\dot{V}_{O_2}$ of *M. formosipes*, I used repeated measures ANOVA, followed by univariate ANOVAs to examine differences among spider conditions at a given temperature. Initially, I used live mass to calculate mass-specific $\dot{V}_{O_2}$. However, because lipids are not as metabolically active as proteins, and spider eggs are lipid-dense (Anderson 1978), I repeated these tests, adjusting mass and metabolic rate of fed spiders to remove the contribution of eggs/lipids. Female spiders accumulate yolk in eggs prior to copulation (Foelix 1996); therefore, I adjusted mass and SMR of fed-virgin as well as fed-gravid *M. formosipes*. For adjusted mass, I used mass measured just after spiders underwent their final molt, assuming that all mass gained between the final molt and the time I measured SMR was due to egg production and fat (yolk) accumulation. (For spiders collected as adults in mid-to-late August, mass at time of collection was used in place of mass at final molt. For spiders collected in September, mass at final molt was estimated based on the percentage of body mass gained between collection and testing of the August-collected adults.) I assumed that eggs and associated lipids had similar $\dot{V}_{O_2}$, and using data of Anderson (1978), I derived an average mass-specific $\dot{V}_{O_2}$ for spider eggs/lipids of 12.8 $\mu l\ g^{-1}\ h^{-1}$ at 15° C. I temperature-corrected egg/lipid mass-specific $\dot{V}_{O_2}$ using individual Q_{10}s for each spider, and subtracted $\dot{V}_{O_2}$ due to eggs/lipids from whole-animal $\dot{V}_{O_2}$ to obtain adjusted $\dot{V}_{O_2}$.

Estimating crab spider SMR from equations relating SMR to body size.—I applied equations relating SMR to live mass, drawn from the literature and derived in this study, to my experimental spiders. Using Mann-Whitney *U*-tests, I compared measured SMR to equation-generated SMR estimates for: 1) each of the three hunger-reproductive conditions of *M. formosipes* considered individually, 2) for *M. formosipes* considered collectively (pooling the three hunger-reproductive conditions together), and 3) for *M. asperata*. Most of the available literature data measured SMR in $\mu l\ O_2\ h^{-1}$ at 20° C. Where oxygen consumption was measured at a different temperature (i.e., Greenstone & Bennett 1982), I converted literature data to 20° C by assuming a Q_{10} of 2.5, as done by Lighton & Fielden (1995). Lighton & Fielden (1995) measured metabolic rate (based on CO_2 production) in μW at 25° C; for comparison, I used my crab spider data collected at 25° C (*M. asperata*), or estimated from individual spider regression equations (*M. formosipes*), and applied a conversion factor of 20.1 J per ml O_2, which assumes a respiratory quotient of 0.8 (Bartholomew 1981), to convert between $\mu l\ O_2\ h^{-1}$, $J\ h^{-1}$, and μW.

To compare the accuracy of the various equations in estimating crab spider SMR in general, I combined data for *M. formosipes* and *M. asperata* and determined the similarity between actual and estimated SMR. I calculated an index of similarity by dividing estimated SMR by measured SMR and used ANOVA to compare similarity scores among mass-metabolism equations.

Generalized spider mass-metabolism relationship.—To examine the general relationship between spider metabolism and live mass, I combined metabolic rates measured for *M. asperata* and *M. formosipes* at 20° C with published data. I used only data that met the criteria for SMR (i.e., spiders were rested and fasting) and selected protocols with three days of fasting as the minimum time period sufficient to ensure that spiders were post-absorptive. Nakamura (1987) showed that spider metabolic rate declines precipitously for the first 2–3 days post-feeding, but levels off by day 3–4, although the gut is not fully empty until approximately six days post-feeding. Data of Anderson (1970, 1996), Greenstone & Bennett (1980), Anderson & Prestwich (1982) and Shillington (2005) met the necessary criteria: these studies typically fasted spiders for 6–7 days; Anderson & Prestwich (1982) fasted spiders 3–7 days, but indicated that all spiders were post-absorptive. The resulting compilation data set comprised 117 data points (individual spiders or species averages) representing 54 species from 18 families. I analyzed the data using the traditional method of linear regression and a newer multiple regression technique described by Meehan (2006), based on Gillooly et al. (2001).

Statistical tests.—I tested all data, including ratios, and confirmed that the data satisfied assumptions of normality and homogeneity of variance: mass, $\dot{V}_{O_2}$, and mass-specific $\dot{V}_{O_2}$ required $\log_{10}$ transformation. Where sample sizes were small, I used nonparametric tests on raw data. I adjusted significance values as needed for multiple comparisons (Bonferroni correction).

RESULTS

Temperature and body size strongly affected crab spider SMR. Manipulation of hunger and reproductive condition successfully generated a wide range of body sizes in *M. formosipes*: while individuals assigned to the various hunger-reproductive conditions were of similar size just after their final molt (Kruskal-Wallis test: $H = 3.708$, $P = 0.1566$), size at time of testing differed significantly (Kruskal-Wallis test: $H = 12.375$, $P = 0.0021$) and varied over a six-fold range (Table 2). Comparison of initial mass and mass at time of testing indicated that eggs/lipids constituted 39% and 68% of the mass of fed-virgin and fed-gravid spiders, respectively.

Table 2.—Mass (mg) of *M. asperata* and *M. formosipes* used in the experiments. Size of experimental spiders is compared to that of recently matured conspecific females. Values for mass are means (± 1 SD). For fed-gravid *M. formosipes* (which were collected as adults), mass at time of collection was used in place of mass at final molt. x = times, in right-hand column.

Spider	*n*	Mass	Mass range	Size relative to newly matured adult
Present study				
Mecaphesa asperata	9	55.5 (10.9)	40.8–71.7	2 x
Misumenoides formosipes	15	98.4 (54.5)	29.7–187.8	2.2 x
At time of testing				
Starved	5	37.7 (8.0)	29.7–47.7	0.86 x
Fed-virgin	6	100.8 (17.1)	79.3–123.1	2.3 x
Fed-gravid	4	170.6 (14.6)	152.2–187.8	3.9 x
At final molt				
Starved	5	45.0 (11.3)		
Fed-virgin	6	60.7 (11.2)		
Fed-gravid	4	54.8 (10.1)		
Comparison data				
Mecaphesa asperata				
Newly matured	72	28.1 (10.1)	10.7–56.2	1 x
Pre-ovipositional	24	61.9 (13.1)	34.2–84.2	2.2 x
Misumenoides formosipes				
Newly matured	176	44.0 (14.7)	10.3–104.8	1 x
Pre-ovipositional	36	149.4 (68.5)	73.7–407.0	3.4 x

Temperature and crab spider SMR.—Temperature strongly affected crab spider SMR (Table 3). Mass-specific $\dot{V}_{O_2}$ of both *M. asperata* and *M. formosipes* increased with increasing temperature, and temperature accounted for > 80% of the variation in metabolic rate. ANCOVA indicated that SMR-temperature relationships of the two crab spider species were nearly identical: neither slopes (ANCOVA, species × temperature) nor intercepts (ANCOVA, species) of the regression lines differed. Comparison of the mass-specific $\dot{V}_{O_2}$-temperature relationships of *M. asperata* and *M. formosipes* with those published for other species (Table 4) revealed that although y-intercepts varied (ANCOVA, source, $F = 292.859$, $P < 0.0001$), slopes were equivalent (ANCOVA, source × temperature, $F=1.855$ $P = 0.1075$).

Temperature coefficients.—SMR of *M. asperata* displayed equivalent Q_{10}s across the experimental temperature range, while SMR of *M. formosipes* showed a significantly higher Q_{10} at low temperature than at mid-range temperature or high temperature (Table 5). Among the three hunger-reproductive conditions of *M. formosipes*, no clear pattern emerged other than that starved spiders tended to have higher Q_{10}s at the upper and lower ends of the experimental temperature range than did fed spiders.

Impacts of temperature, hunger, and reproductive condition on SMR of *M. formosipes*.—Hunger-reproductive condition and temperature significantly affected mass-specific $\dot{V}_{O_2}$ of *M. formosipes* (Table 6). When I used live mass to calculate mass-specific $\dot{V}_{O_2}$, I found that fed-gravid spiders typically had significantly lower mass-specific $\dot{V}_{O_2}$ at all temperatures except 10° C (Fig. 1A). When I removed the contributions of eggs/lipids to mass and SMR of fed spiders, I found that starved spiders generally had lower mass-specific SMR than fed

Table 3.—ANCOVA and linear regressions of temperature impacts on mass-specific SMR of *M. asperata* and *M. formosipes*. Temperature (T_a in the regression equation) was measured in ° C. Metabolic rate ($\dot{V}_{O_2}$ in the regression equation) was measured as oxygen consumption in $\mu l\ g^{-1}\ h^{-1}$ using live mass.

Test	*F*	*df*	r^2	*P*	regression equation
ANCOVA:					
Spider species	0.007	1		0.9348	
Temperature	541.023	1		< 0.0001	
Species x temperature	0.019	1		0.8913	
Linear Regression:					
Both species combined	592.293	1, 117	0.835	< 0.0001	$\log \dot{V}_{O_2} = 1.405 + 0.033\ T_a$
Mecaphesa asperata	253.352	1, 58	0.814	< 0.0001	$\log \dot{V}_{O_2} = 1.407 + 0.033\ T_a$
Misumenoides formosipes	292.455	1, 58	0.835	< 0.0001	$\log \dot{V}_{O_2} = 1.413 + 0.033\ T_a$
Starved	173.59	1, 18	0.906	< 0.0001	$\log \dot{V}_{O_2} = 1.322 + 0.038\ T_a$
Fed-virgin	162.62	1, 22	0.881	< 0.0001	$\log \dot{V}_{O_2} = 1.538 + 0.031\ T_a$
Fed-gravid	128.546	1, 14	0.902	< 0.0001	$\log \dot{V}_{O_2} = 1.338 + 0.030\ T_a$

Table 4.—Mass-specific SMR-temperature regression equations presented in the literature or derived from literature data. SMR ($\dot{V}_{O_2}$ in the regression equations) was measured as oxygen consumption in μl g^{-1} h^{-1} and was based on live spider mass. Temperature (T_a in the regression equations) was measured in ° C. Average value for the slopes (semi-log) of the SMR-temperature regressions, including those for *M. asperata* and *M. formosipes*, was 0.035 (SE = 0.002).

Literature source & spider	Regression equation	Derivation of regression equation
Moulder & Reichle (1972)		
thomisids, gnaphosids, lycosids	$\log \dot{V}_{O_2} = 1.696 + 0.032\ T_a$	Given in paper
Seymour & Vinegar (1973)		
Aphonopelma sp.	$\log \dot{V}_{O_2} = 1.065 + 0.029\ T_a$	Estimated from Fig. 2 data, 10–40° C
	$\log \dot{V}_{O_2} = 0.754 + 0.038\ T_a$	Estimated from Fig. 3 data, 20–40° C
Anderson (1970)		
Lycosa lenta	$\log \dot{V}_{O_2} = 1.087 + 0.042\ T_a$	Calculated from Table 5 data, 10–30° C
Phidippus regius	$\log \dot{V}_{O_2} = 1.155 + 0.040\ T_a$	Calculated from Table 5 data, 10–30° C
Filistata hibernalis	$\log \dot{V}_{O_2} = 0.738 + 0.048\ T_a$	Calculated from Table 5 data, 10–30° C
Moeur & Eriksen (1972)		
Lycosa carolinensis		
January spiders	$\log \dot{V}_{O_2} = 1.595 + 0.026\ T_a$	Calculated from Table 1 data: 23.5° C, 29° C, 35° C, 39° C, 45° C
June spiders	$\log \dot{V}_{O_2} = 1.491 + 0.025\ T_a$	Calculated from Table 1 data: 29° C, 35° C, 39° C, 45° C

spiders (Fig. 1B); whole animal $\dot{V}_{O_2}$ showed a similar pattern (Fig. 1C). Mass of starved spiders was significantly lower than adjusted mass of fed spiders (Kruskal-Wallis test: $H = 8.312$, $P = 0.0152$), averaging 65% of that of fed spiders. Whole animal $\dot{V}_{O_2}$ of starved spiders averaged 37% that of fed spiders (comparison of raw data, $\dot{V}_{O_2}$ of fed spiders adjusted to remove egg/lipid contributions).

Estimating crab spider SMR from equations relating SMR to body size.—With the notable exception of Hemmingsen's equation, the various mass-metabolism equations predicted crab spider SMR reasonably well (Fig. 2). The significant ANOVA ($F = 10.723$, $df = 8$, $P < 0.0001$) was driven by Hemmingsen's equation, which consistently over-estimated crab spider SMR. No differences in average predictive ability occurred among the other equations.

The various equations did not predict measured SMR of individual species, or hunger-reproductive conditions of *M. formosipes*, equally well (Table 7). Measured SMR of *M. asperata* was lower than all estimates, often significantly so. In contrast, estimates were generally equivalent to measured SMR of *M. formosipes* (considered collectively). Of the hunger-reproductive conditions of *M. formosipes*, the various equations usually predicted SMR of starved spiders quite well, but tended to under-estimate SMR of fed-virgin spiders and over-estimate SMR of fed-gravid spiders.

Generalized spider mass-metabolism relationship.—Both linear regression and multiple regression generated mass-scaling exponents of approximately 0.67: linear regression, $F = 706.546$, $df = 1,117$, $r^2 = 0.86$, $P < 0.0001$, $\log \dot{V}_{O_2} = -0.132 + 0.654\ (\log M)$ or $\dot{V}_{O_2} = 0.738\ M^{0.654}$, where $\dot{V}_{O_2}$ is oxygen consumption (μl h^{-1}) and M is mass (mg); multiple regression, $F = 364.97$, $df = 2,114$, $r^2 = 0.865$, $P_{total} < 0.0001$, $P_{intercept} = 0.0013$, $P_{mass} < 0.0001$, $P_{temp} = 0.0005$, $ln\ \dot{V}_{O_2} = 48.421 + 0.667\ (ln\ M) - 1.334\ (1/kT)$, where $\dot{V}_{O_2}$ is oxygen consumption (J h^{-1}), M is mass (mg), k is Boltzmann's constant (0.0000862), and T is temperature (K). (Note: in the latter portion of the multiple regression equation, units cancel out because 1.334 has units of eV and Boltzmann's constant has units of eV K^{-1}.) SMR of *M.*

Table 5.—Temperature coefficients (Q_{10}s) of *M. asperata* and *M. formosipes* across the experimental temperature range. Values presented are means (± 1 SD). I used Kruskal-Wallis tests to compare Q_{10} values within a given species. I also compared Q_{10} values within a given temperature interval among *M. formosipes* hunger-reproductive conditions (adjusted $\alpha \leq 0.0167$, Bonferonni correction for multiple comparisons). If Kruskal-Wallis tests were significant, I used Mann-Whitney U-tests to make pair-wise comparisons: values with different letters are significantly different ($P \leq 0.05$).

	Temperature interval			
Spider	10–20° C	20–30° C	30–40° C	Kruskal-Wallis *P*
Mecaphesa asperata Q_{10}	2.35 (0.84)	2.04 (0.94)	2.40 (0.96)	0.4498
Misumenoides formosipes Q_{10}	3.90 (0.72)[a]	1.69 (0.40)[b]	1.75 (0.52)[b]	< 0.0001
M. formosipes categories:	Starved Q_{10}	Fed-virgin Q_{10}	Fed-gravid Q_{10}	
Temperature interval				
10–20° C	4.32 (0.55)	4.03 (0.73)	3.20 (0.34)	0.0463
20–30° C	1.72 (0.55)	1.55 (0.27)	1.87 (0.37)	0.2563
30–40° C	2.22 (0.52)	1.61 (0.36)	1.38 (0.31)	0.0435

Table 6.—Repeated measures ANOVA examining impacts of temperature (°C) and spider condition on mass-specific SMR [log ($\mu l\ O_2\ g^{-1}\ h^{-1}$)] of *M. formosipes*. Tests were run on data calculated using live spider mass and on data in which mass and SMR of fed spiders were adjusted to remove contributions of eggs/lipids. Associated univariate ANOVAs comparing mass-specific SMR among spider conditions at a given temperature are also provided. For univariate ANOVAs, a significant difference occurs at $\alpha \leq 0.0125$ (Bonferroni correction for multiple comparisons).

Test and effect	*df*	*F*	*P*
Live mass			
Repeated measures ANOVA			
Spider condition	2	20.011	< 0.0001
Temperature	3	541.291	< 0.0001
Interaction	6	3.736	0.0054
Univariate ANOVAs			
10° C	2	4.401	0.0368
20° C	2	12.946	0.0010
30° C	2	9.572	0.0033
40° C	2	32.896	< 0.0001
Adjusted mass & SMR			
Repeated measures ANOVA			
Spider condition	2	48.921	< 0.0001
Temperature	3	541.799	< 0.0001
Interaction	6	3.727	0.0055
Univariate ANOVAs			
10° C	2	22.921	< 0.0001
20° C	2	18.758	0.0002
30° C	2	28.586	< 0.0001
40° C	2	7.625	0.0073

asperata and *M. formosipes* at 20° C fit well within the general scatter of literature data (Fig. 3).

DISCUSSION

Temperature strongly affected crab spider SMR. As predicted, mass-specific $\dot{V}_{O_2}$ increased with increasing temperature, and Q_{10}s reflected temperature impacts on crab spider hunting performance. Whole-animal $\dot{V}_{O_2}$ increased with increasing body size, as expected, but contrary to my prediction, mass-specific $\dot{V}_{O_2}$ of *M. formosipes* differed with hunger or reproductive condition, and the precise impact depended on the nature of the mass-specific $\dot{V}_{O_2}$ calculation. Spider SMR scaled as 2/3 of live body mass, and most mass-metabolism equations generated reasonable estimates of (collective) crab spider SMR; however, estimates were not as accurate for fed spiders (mated or virgin) as they were for starved spiders. These results point to the need for caution when evaluating spider SMR: accurate assessment requires knowledge of spider hunger and reproductive condition.

Temperature and crab spider SMR.—Given that spiders are strict ectotherms (Pulz 1987), a strong impact of temperature on SMR of *M. asperata* and *M. formosipes* was expected. Nor was it surprising that neither degree of hunger nor reproductive condition affected the general nature of the temperature-metabolism relationship. Many studies have shown that metabolic rate increases with increasing temperature in spiders and other terrestrial arthropods (Anderson 1970; Moulder & Reichle 1972; Seymour & Vinegar 1973; Humphreys 1975; Lighton et al. 2001; Meehan 2006). The slope of the regression line relating mass-specific $\dot{V}_{O_2}$ to temperature is remarkably consistent among spider species, suggesting a relatively high degree of conformity among spiders in their response to temperature.

Temperature coefficients.—Q_{10}s describe the effects of temperature changes on the rates of physiological processes or biochemical reactions (Hochachka & Somero 1984; Wilmer et al. 2005), and metabolic rates typically have Q_{10}s of 2–3 (Wilmer et al. 2005). As predicted, Q_{10}s for crab spider SMR correlated with temperature impacts on spider hunting performance. Q_{10}s for SMR of *M. asperata* varied between 2.0–2.4 across the experimental temperature range, suggesting that *M. asperata* is active and functions normally between 10–40° C. In contrast to *M. asperata*, SMR of *M. formosipes* showed a significantly higher Q_{10} at low temperature than at moderate temperature or high temperature. High Q_{10} at low temperature is a common response in ectotherms (Hoffman 1985) and has been proposed as a means of conserving energy during thermally unfavorable periods (e.g. Aleksiuk 1976); as temperature increases, a greater-than-normal increase in metabolic rate allows normal activity to resume quickly. The dramatic increase in $\dot{V}_{O_2}$ of *M. formosipes* occurring between 10–20° C suggests that *M. formosipes* is not normally active at 10° C. The difference between the two crab spider species in Q_{10} at low temperature also correlates with seasonal differences in temperature during the species' adult and penultimate instars, with *M. formosipes* experiencing temperatures averaging 5° C higher than those experienced by *M. asperata*.

Impacts of temperature, hunger, and reproductive condition on SMR of *M. formosipes*.—Manipulation of hunger and reproductive condition produced spiders that differed significantly in mass at the time of testing, although they had been of similar initial mass. Neither hunger nor reproductive condition changed the general nature of the temperature-$\dot{V}_{O_2}$ relationship in *M. formosipes*; metabolic rate increased with increasing temperature, and regression slopes were similar among all three conditions. Hunger or reproductive condition did, however, have a significant impact on mass-specific $\dot{V}_{O_2}$, and the nature of the effect depended on whether I used live mass or whether I removed the contribution of eggs/lipids when calculating mass-specific $\dot{V}_{O_2}$.

Using live mass, temperature interacted with spider condition to affect $\dot{V}_{O_2}$; mass-specific SMR of *M. formosipes* did not differ among conditions at 10° C, but at all other temperatures, fed-gravid spiders had lower mass-specific $\dot{V}_{O_2}$ than fed-virgin or starved spiders. The similarity among conditions at 10° C could reflect a general suppression of metabolic rate at low temperature in *M. formosipes*. At higher temperatures, the lower mass-specific $\dot{V}_{O_2}$ of fed-gravid spiders resulted from the large contribution of egg mass to total body mass. Anderson (1978) found that free-living spiders had metabolic rates almost an order of magnitude higher than those of developing eggs. Eggs held within a female's body prior to oviposition should likewise be relatively metabolically inert. Because fats are less metabolically active than proteins, and spider eggs contain a large amount of lipid (Anderson 1978), the more egg-heavy the spider, the greater the proportionate contribution of lipid-dense tissue to overall body mass, and, consequently, the lower the mass-specific $\dot{V}_{O_2}$

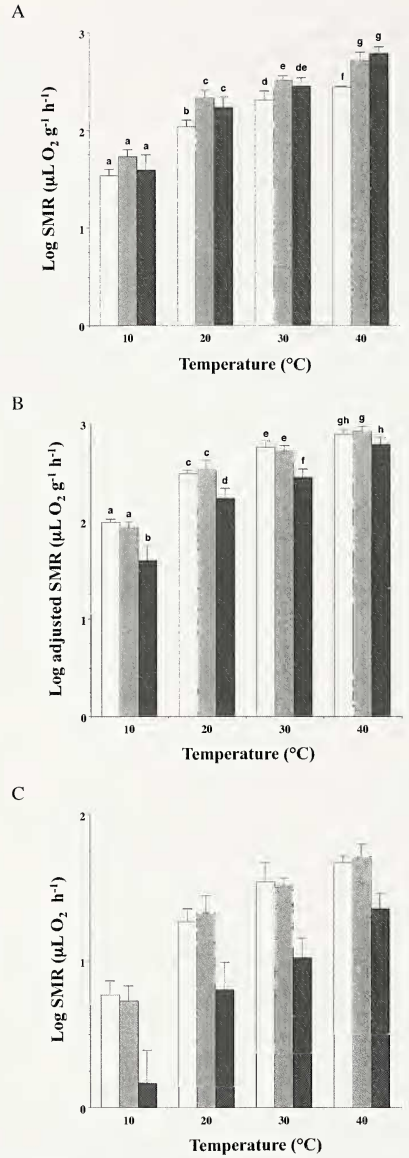

Figure 1.—Average SMR of *M. formosipes* hunger-reproductive conditions across the experimental temperature range. Within a test temperature, values with different letters are significantly different at $\alpha \leq 0.0125$ (Bonferroni correction for multiple comparisons) using a Bonferroni-Dunn post-hoc test. Comparisons were made only among hunger-reproductive conditions within a given temperature, not across temperatures. Error bars = 1 SD. Symbols: □ = fed-gravid, ■ = fed-virgin, ■ = starved. A. Mass-specific SMR calculated using live mass. At 30° C, starved and fed-gravid spiders were nearly significantly different ($P = 0.0127$). B. Mass-specific SMR calculated using adjusted mass and SMR for fed spiders (contributions of eggs/lipids removed). At 40° C, starved and fed-gravid spiders were nearly significantly different ($P = 0.0194$). C. Whole-animal SMR provided for comparison; SMR of fed spiders has not been adjusted to remove contributions of eggs/lipids.

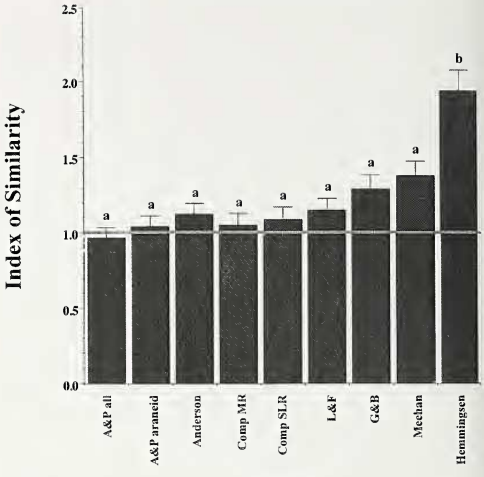

Figure 2.—Average similarity between measured crab spider SMR (*M. asperata* and *M. formosipes* combined) and SMR estimated using mass-metabolism equations. I calculated the index of similarity as estimated SMR divided by measured SMR. The closer to one an equation's similarity score, the better it predicted crab spider SMR. Values with different letters are significantly different at $\alpha \leq 0.05$ (Scheffé post-hoc test). Error bars = 1 SE. A&P all = Anderson & Prestwich (1982) all spiders; A&P araneid = Anderson & Prestwich (1982) araneids only; Anderson = Anderson (1996) thomisids; Comp MR = compilation data set, multiple regression (this study), spiders; Comp SLR = compilation data set, linear regression (this study), spiders; L&F = Lighton & Fielden (1995) arthropods (ants, beetles, spiders); G&B = Greenstone & Bennett (1980) spiders; Meehan = Meehan (2006) arthropods (orobatid mites, springtails, spiders); Hemmingsen = Hemmingsen (1960) ectotherms.

compared to non-gravid spiders whose body composition is proportionately less lipid-dense. Approximately two-thirds of the mass of fed-gravid *M. formosipes* consisted of eggs. This is typical of flower-dwelling crab spiders: other studies have found that eggs constitute more than 60% of female pre-oviposition weight (Fritz & Morse 1985; Beck & Connor 1992; Schmalhofer unpubl. data).

Mass-specific $\dot{V}_{O_2}$ does not totally eliminate the influence of body size on metabolic rate because mass and metabolism share an allometric relationship (Packard & Boardman 1999). ANCOVA on whole-animal $\dot{V}_{O_2}$, with mass as the covariate,

Table 7.—Comparison of measured SMR of *M. asperata* and *M. formosipes* with estimated SMR based on various mass-metabolism equations: Lighton & Fielden (1995), arthropods, $\dot{V}_{O_2} = 906M^{0.825}$; Anderson (1996), *M. formosipes*, $\dot{V}_{O_2} = 0.62M^{0.7}$, *M. celer*, $\dot{V}_{O_2} = 0.52M^{0.71}$; Anderson & Prestwich (1982), all spiders, $\dot{V}_{O_2} = 0.33M^{0.8}$, araneids, $\dot{V}_{O_2} = 0.18M^{0.96}$; Greenstone & Bennett (1980), spiders, $\dot{V}_{O_2} = 0.736M^{0.71}$ at 22° C, $\dot{V}_{O_2} = 0.698M^{0.71}$ at 20° C; Meehan (2006), arthropods, $ln(\dot{V}_{O_2}) = 18.42 + 0.77\ [ln(M)] - 0.58$ (l/kT); Hemmingson (1960), ectotherms, $\dot{V}_{O_2} = 0.82M^{0.75}$; compilation SLR (this study), spiders, $\dot{V}_{O_2} = 0.738M^{0.654}$; compilation MR (this study), spiders, $ln(\dot{V}_{O_2}) = 47.354 + 0.677\ [ln(M)] - 1.308$ (l/kT). Anderson's (1996) equations for *M. formosipes* and *M. celer* were compared to *M. formosipes* and *M. asperata*, respectively. For Meehan (2006) and the compilation multiple regression, $\dot{V}_{O_2}$ was calculated in J h^{-1}, but converted back to µl h^{-1} for this table. Comparisons with Lighton & Fielden (1995) were made in µW at 25° C. Mann-Whitney *U*-tests were used to compare measured values with equation-generated estimates: a significant difference occurs at $\alpha \leq 0.0056$ (Bonferroni correction for multiple comparisons). Values presented are means (±1SD). †$P \leq 0.05$, *$P \leq 0.0056$.

Source	*Mecaphesa asperata*	*Misumenoides formosipes*			
		All	Starved	Fed-virgin	Fed-gravid
Measured SMR					
µl h^{-1} at 20° C	7.7 (1.7)	16.1 (7.9)	6.9 (3.3)	21.9 (5.2)	19.0 (3.8)
µW at 25° C	64.9 (26.8)	130.7 (53.2)	64.1 (17.1)	167.0 (24.7)	159.4 (25.6)
Estimated SMR					
Lighton & Fielden (1995)	83.7 (12.7)	130.8 (61.6)	60.5 (10.6)	136.2 (18.0†)	210.6 (14.9)†
Anderson (1996)	9.0 (1.2)	14.9 (6.1)	7.8 (1.2)	15.6 (1.8)	22.6 (1.4)
Anderson & Prestwich (1982)					
All spiders	8.2 (1.2)	12.7 (5.8)	6.0 (1.0)	13.2 (1.7)	20.1 (1.4)
Araneids	8.6 (1.5)	14.7 (7.8)	5.9 (1.2)	15.1 (2.3)†	25.0 (2.1)†
Greenstone & Bennett (1980)	12.8 (1.7) *	18.5 (7.7)	9.7 (1.5)	19.4 (2.2)	28.3 (1.7)†
Meehan (2006)	11.8 (1.7) *	17.8 (7.9)	8.7 (1.4)	18.6 (2.3)	28.0 (1.8)†
Hemmingsen (1960)	16.7 (2.3) *	24.9 (10.8)†	12.4 (2.0)†	26.0 (3.1)	38.7 (2.5)†
Compilation SLR	9.5 (1.2) †	13.4 (5.1)	7.4 (1.0)	14.0 (1.5)†	19.9 (1.1)
Compilation MR	9.2 (1.1)†	13.0 (5.1)	7.1 (1.0)	13.4 (1.5)†	19.4 (1.1)

can resolve this issue (Packard & Boardman 1988, 1999). However, an underlying assumption of using ANCOVA is that all mass behaves similarly with respect to impacts on metabolic rate. This was not the case for these spiders, since a large fraction of the mass of fed spiders was a composed of metabolically inactive tissue that contributed little to total metabolism. Adjusting mass and metabolism to exclude the influence of non-metabolizing tissue before examining mass-specific SMR was a more appropriate, although not perfect, solution.

Removing the estimated contribution of eggs/lipids to mass and SMR of fed spiders revealed that starved *M. formosipes* had lower mass-specific $\dot{V}_{O_2}$ than fed spiders. Reductions in metabolic rate attributed to starvation by many authors actually reflect attainment of a post-absorptive state in which energy is no longer being used for digestion and assimilation (Nakamura 1987). True suppression of metabolic rate as a consequence of prolonged starvation, as reported by Anderson (1974), has seldom been shown. I found that the percent reduction in $\dot{V}_{O_2}$ of starved *M. formosipes* was comparable to that measured by Anderson (1974) for starved *Kukulcania hibernalis* (Hentz 1842) (as *Filistata hibernalis*) and *Hogna lenta* (Hentz 1844) (as *Lycosa lenta*): at 20° C, mass-specific SMR was reduced by 32% in *H. lenta*, 40% in *K. hibernalis*, and 47% in *M. formosipes*. (Because Anderson's study involved non-fat, non-reproductive spiders, my results were not directly comparable until I adjusted for egg/lipid contributions to mass and $\dot{V}_{O_2}$.) It is possible that the reduction in SMR seen in starved *M. formosipes* was a result of decreased mass rather than physiologic changes associated with prolonged starvation. Starved spiders lost 15% of body mass during the fasting period and had lower mass than fed spiders, even after removal of egg/lipid mass from the latter, so mass was not "equalized" among treatment groups. However, it seems likely that the reduced metabolic rate observed in starved *M. formosipes* was an effect of starvation beyond loss of mass: differences between fed and starved spiders in mass and $\dot{V}_{O_2}$ were disproportionate (mass and $\dot{V}_{O_2}$ of starved spiders averaged 65% and 37%, respectively, of that of fed spiders), whereas differences between mass and $\dot{V}_{O_2}$ of fed-gravid and fed-virgin spiders were proportionate. Hence, true starvation-induced suppression of metabolic rate, as seen in long-lived, iteroparous species (Anderson 1974), also appears to occur in the short-lived, semelparous *M. formosipes*. It may be that starvation-induced suppression of metabolism is a general phenomenon in spiders; further studies with other species are needed.

Elevation of metabolic rate as a consequence of reproductive condition has been shown in various ectothermic species, such as rattlesnakes (Beaupre & Duvall 1998) and lizards (Angilleta & Sears 2000). Walker & Irwin (2006) predicted that spiders would behave similarly, with reproductive females having higher mass-specific metabolic rates than non-reproductive females. My data did not support this hypothesis: mass-specific $\dot{V}_{O_2}$ of fed-gravid *M. formosipes* was equivalent to or lower than that of fed-virgin *M. formosipes*. *Misumenoides formosipes* is not unique in this respect: differences in metabolic rates of reproductive and non-reproductive mites have also been found to be explicable on the basis of body mass (Young & Block 1980). Why spiders and mites differ from vertebrate ectotherms in this regard is not clear.

Estimating crab spider SMR from equations relating SMR to body size.—With the notable exception of Hemmingsen's equation, the various mass-metabolism equations were statistically indistinguishable from one another and, on average, provided reasonably accurate estimates of crab spider SMR,

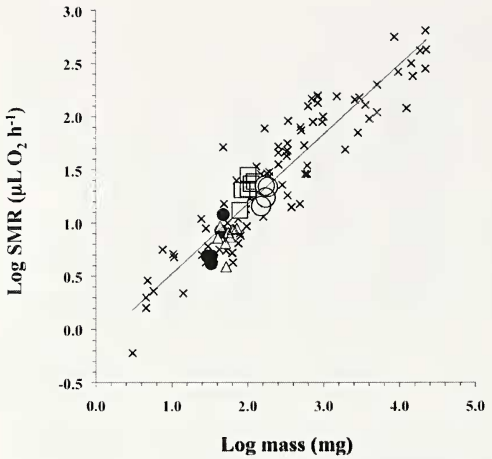

Figure 3.—Relationship between spider SMR and live mass at 20° C. Each data point represents an individual spider or a species average. I determined the regression line using linear regression: log $\dot{V}_{O_2}$ = −0.132 + 0.654 (log M). Literature sources: Greenstone & Bennett (1982), 47 individuals; Anderson (1970), 6 species averages and 15 individuals; Anderson (1996), 12 species averages; Anderson & Prestwich (1982), 12 species averages; Shillington (2005), 1 species average. Data for Anderson & Prestwich were estimated from Anderson & Prestwich (1982), Figure 1; the resulting mass-metabolism equation based on these estimates ($\dot{V}_{O_2}$ = 0.321 $M^{0.802}$) was nearly identical to the equation derived by Anderson & Prestwich ($\dot{V}_{O_2}$ = 0.33 $M^{0.8}$). Symbols: ×= literature data, ●= *Misumenoides* starved, □= *Misumenoides* fed-virgin, ○= *Misumenoides* fed-gravid, △= *Mecaphesa*.

based on live mass. Most of the equations generated estimates of crab spider metabolic rate that were somewhat higher than actual measured values. Hemmingsen's equation, however, greatly over-estimated crab spider SMR, yielding estimates that were nearly double actual values and significantly larger than other estimates. Similar results when comparing spider metabolic rates with estimates based on Hemmingsen's equation are common (e.g. Anderson 1970; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Strazny & Perry 1987). Hemmingsen (1960) has frequently been cited for comparative purposes due to its comprehensive nature (Anderson 1970) and because it expanded the study of metabolic mass scaling to include ectotherms (Dodds et al. 2001; White & Seymour 2005). Widespread use of Hemmingsen's equation as a yardstick for comparison led to the general conclusion that spiders have exceptionally low metabolic rates for arthropods of their size (Anderson 1970; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Strazny & Perry 1987). The utility and validity of Hemmingsen's equation have come into question (Lighton & Fielden 1995; Dodds et al. 2001), however, and spider metabolic rates have been found not to differ from those of non-spider arthropods (Lighton & Fielden 1995; Meehan 2006).

When considering how well the various mass-metabolism equations predicted SMR of a particular crab spider species or hunger-reproductive condition of *M. formosipes*, I obtained mixed results. Over-estimates of SMR generated for fed-gravid *M. formosipes* generally balanced out under-estimates calculated for fed-virgin spiders. Combined with the accuracy of estimates for starved spiders, the equations typically yielded fairly accurate estimates of metabolic rate for *M. formosipes* in total. SMR of *M. asperata*, in contrast, was not as well predicted. I did not manipulate reproductive condition in this species, but body mass suggested that most *M. asperata* were gravid, and, like fed-gravid *M. formosipes*, actual SMR was lower than estimated SMR. To circumvent reproductive complications in evaluating metabolic rate, one needs to exclude the contribution of eggs and associated lipids to total body mass and to express metabolic rate in terms of adjusted "egg/lipid free" mass. In the present study, once I removed egg/lipid mass I found that starved spiders, not fed-gravid spiders, had the lowest mass-specific $\dot{V}_{O_2}$.

The technique of excluding metabolically inactive tissue from metabolic rate measurements has yielded interesting results in other contexts. Djawden et al. (1997) found that stressed lineages of fruit flies had lower mass-specific SMR than non-stressed control lineages and suggested that differential accumulation of lipids and carbohydrates was the cause; they also suggested that fundamental changes in metabolic rate were best detected by expressing metabolic rate in a manner that did not include the mass of non-metabolizing material, and when they accounted for non-metabolizing sources, the differences in metabolic rates between stressed and non-stressed lineages disappeared.

Generalized spider mass-metabolism relationship.—One of the most contentious issues in environmental physiology involves the determination of what constitutes a "characteristic" metabolic rate for an animal of a given size (Chown & Nicholson 2004). The relationship between mass and metabolism is generally described by the allometric equation

$$V = aM^b,$$

which may also be written as

$$\log V = \log a + b(\log M),$$

where V is metabolic rate, M is body mass, and a and b are the intercept and slope, respectively, of the mass-metabolism regression. The value of b is of particular interest. The original null model, first proposed in the 1800s and based on simple dimensional analysis, hypothesizing that b = 0.67, was supplanted in the early 1900s by empirical studies indicating that b = 0.75 (see review by White & Seymour 2005). Aspects of some of the early work widely cited in support of a 3/4 scaling exponent (e.g. Kleiber 1932; Brody 1945; Hemmingsen 1960) have been questioned (e.g. Lighton & Fielden 1995; Dodds et al. 2001; White & Seymour 2005). Consequently, the value of b, which had been accepted as 0.75 for decades, has been subject to re-evaluation, with some authors supporting b = 0.67 (e.g. Dodds et al. 2001; White & Seymour 2005), others maintaining that b = 0.75 (e.g. West et al. 1997; Gillooly et al. 2001; West & Brown 2005), and still others arguing in favor of an entirely different exponent for particular groups of animals. For instance, Lighton et al. (2001) suggest that the mass-scaling exponent for non-tick, non-scorpion arthropods is 0.856. In the present study, I found that SMR of spiders scales as approximately 2/3 of live body mass, regardless of method

used: linear regression, $b = 0.654$ (SE = 0.025); multiple regression, $b = 0.677$ (SE = 0.025). If SMR values for individuals of a given species within a study were averaged in order to reduce the over-representation of particular species in the compilation data set, sample size of the compilation data set was reduced to 60, but b still approximated 2/3: linear regression, $b = 0.668$ (SE = 0.035); multiple regression, $b = 0.678$ (SE = 0.036).

Conclusions.—Temperature exerted a strong impact on crab spider metabolic rate, and temperature impacts on *M. formosipes* and *M. asperata* were comparable to those found for other spider species. Prolonged starvation resulted in a decrease in SMR of *M. formosipes* beyond that which normally occurs as spiders attain a post-absorptive state. Mass-specific $\dot{V}_{O_2}$ of fed-gravid *M. formosipes* was lower than or equivalent to that of fed-virgin *M. formosipes* (depending on how mass-specific SMR was calculated). The low metabolic rate of egg-heavy females, when live mass was used to calculate mass-specific $\dot{V}_{O_2}$, was an artifact of the large contribution of lipid-rich, metabolically-inactive eggs to female mass. Because this effect is expected to be universal among spiders, caution should be exercised when interpreting the results of spider metabolic rate measurements, and reproductive condition of adult female spiders should be taken into account. Ideally, in experiments investigating how factors that affect body size ultimately affect metabolic rate, pre-treatment and post-treatment metabolic rates should be determined so that treatment effects can be compared against a true baseline measure. A control group fed a diet designed to maintain constant body mass should also be used to account for potential impacts of time (aging) on the animals.

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